ORIGINAL PAPER

Territory and territorial behavior of migrating Common Coot (Fulica atra)

ZHANG Wei-wei • LIU Wei • MA Jian-zhang

Received: 2010-02-21; Accepted: 2010-05-15

© Northeast Forestry University and Springer-Verlag Berlin Heidelberg 2011

Abstract: Territory and territorial behavior of the Common Coot (Fulica atra) were studied in two breeding sites, Anbanghe Nature Reserve and Daqing Longfeng wetland, in Heilongjiang Province, China from April to October in 2008 and 2009. In the breeding season, the breeding pairs occupied an area and protected it throughout the reproduction, and both interspecific and intraspecific conflicts were observed. Territory activities became severe since early May, the peak of territory behaviors appeared at late May, and then declined gradually. The territorial activities level was higher than that in the nest building period than in the laying and incubation periods. The most adopted behavioral model was expelling, which was the least energy cost. The degree of territorial behavior tended to be descended since the development of breeding phase. The territory size differed from 1 333 m² to above 5 000 m². Wintering population was observed in Poyang Lake of Jiangxi Province. The coots gathered in the open water; however, there was no territory behavior both in the interspecies and intraspecies in wintering sites. The hypotheses why there was territory behaviors for coots both in the interspecies and intraspecies were also discussed.

Keywords: The Common Coot (*Fulica atra*); territoriality; territorial behavior; territory size; breeding, migrating

Introduction

Territorial behavior, a type of aggressive behavior attached to a

Foundation project: This work was supported by Natural Science Foundation of Heilongjiang Province (C201036)

The online version is available at http://www.springerlink.com

ZHANG Wei-wei • LIU Wei

College of Landscape and Art, Jiangxi Agricultral University, Nanchang, 330045, China. E-mail: zhangweiwei_nefu@163.com

ZHANG Wei-wei • MA Jian-zhang (M)

College of Wildlife Resources, Northeast Forestry University, HarBin, 150040, China. E-mail: jianzhangma@163.com

Responsible editor: Yu Lei

certain area (Tinbergen 1957; Stephan 1976), has been reported in many groups of birds. Territorial animals live in a network of conspecific rivals competing with each other for accessing to resources and for the attention of potential mates (Hyman et al. 2006).

F. atra is an abundant and prolific aquatic bird. For the resident population, F. atra maintains territory activities all the year, including winter, and generally the area defended in winter is somewhat larger than that required for breeding (Huxley 1934). F. atra is different from the American Coot (Fulica Americana), whose core areas of winter territories account for 6.5%–59% of the fully expanded summer territories (Gullion 1953). Cavé et al. (1989) studied the size and quality of F. atra territory in relation to age of its tenants and neighbours. The results show that old pairs arrived earlier and had larger territories compared to young pairs. Visser (1988) found that the white frontal shield (a display structure used in competitor assessment) of F. atra is larger in old birds than in young ones (Visser 1988).

Gullion (1953) reported that American Coot had a peak of territory behaviors in brooding period, but the situation for *F. atra* was not known clearly. In China, the distribution of *F. atra* covers almost all the parts of the country; however, no substantive research was carried out on its territoriality, the territory size and its variation.

Study site and methods

From early May to late May in 2008 and 2009, two breeding populations of *F. atra* were monitored during three periods of reproduction at Anbanghe Nature Reserve (131°06'E–131°32'E and 46°53'N–47°03'N) and Daqing Longfeng wetland (125°07'E–125°15'E and 46°28'N–46°32'N) in Heilongjiang Province, China. The emergent plants of two study sites are similar, dominated by reed (*Phragmites australis*) and cattail (*Typha angustifolia*), broadleaf Cattail (*Typha latifolia*) and calamus (*Acorus calamus*).

Eleven pairs of coots at three different breeding stages (nest building, laying and incubation) were observed using a binocular



telescope (8×42) with all-occurrence recording and focal animal sampling methods. The sex of individuals was identified by their voice and frontal shield characteristics according to the differences described in the studies of the American Coot (Gullion 1950, 1951; Fredrickson 1968; Eddleman et al. 1985). Combined with territorial behavior, body size, calls and behavior patterns, the sex and individuals were also determined.

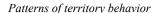
The coots whose territories were near the edge of lake or pond were chosen because the cover of lake edge was thin and the bird movements were easier to trace. For convenient monitoring, the observation points, where there was no obvious effect on the birds' normal behavior, were chosen at less than 200 m from the breeding pairs. Total 11 pairs of coots in different stages of breeding were observed every day during May when the new plant growth (i.e., reeds and cattails) was relatively short and thin. Full day observation and recordings were performed every day from 5:00 to 17:00 in May at Anbanghe Reserve and Longfeng wetlands. Observations terminated before the young were hatched. Among the 11 pairs of coots, four pairs (A, B, C and D) were in nest building period, two pairs (E and F) were in laying period, and five pairs (G, H, I, J, K) were in incubation period.

In general, the pairs distributed in the edge have larger territories, in which the territory size of coots would be overrated. Average territorial areas were obtained by finding all the nests in two small ponds whose area were known (DQ and YJ, where there were the available areas fully used.). Meanwhile, four quadrats were plotted in a big pool of Anbanghe (YF1-4). In each quadrat, there were appropriate vegetations and water, and each quadrat was isolated by big water surface respectively to insure that there were no coots' territories connected with outside quadrat. All nests were found out in the four quadrats for the calculation of the average territory size. Territory boundaries were determined by extensive observation of the patrol action locations and the interactions location between neighbors such as fighting and warning. Conflict sites were marked on the coordinate paper, and localized using GPS. All sightings and observations of aggressive encounters with neighbors and other waterfowl were mapped. Territory size of the coots was calculated by Mapsource 7.6. Statistical analysis was made in EXCEL, Sigma Plot 10.0 and SPSS 17.0.

Results

Aggressive territory behaviors of the breeding pairs

The paired coots occupied a territory and protected it throughout the breeding period. Non breeding individuals gathered in neutral open water without territoriality, and they were always attacked by breeding pairs at the edge of vegetation. These floaters obtained territories occasionally, and then began to nest after pairing and exhibiting territoriality. In the pool of Anbanghe, more than 200 coots gathered in the open water in early May, while the others were paired and dispersed. The amount of coots decreased to about 100 till September.



Gullion (1952) described 11 kinds of the display of the American Coot, which were also suitable for *F. atra*. Of 11 kinds of display, six kinds of display were related to the territory defense. They were adopted alone or in the mixed ways. There are three main activities in territory defenses of F. atra, warning, expelling, and fighting. For warning, head is down to water surface, primaries are held up at the back, and tail feathers fluff. This behavior is always being adopted when neighbors approach the resident's territorial boundary, and its partner always hurries to the strife point for support from other place in their territory. This behavior is normally the final action of aggression. For expelling, the host rushes a distance to attack the intruders, when the territory is intruded into. For fighting, neighbors at the boundary of territories fight with each other when the conflict becomes severe. Their feet hook, wings extend, and one pecks the other's head. These behaviors usually last for less than one minute.

Interspecific conflicts during the breeding seasons

F. atras seeks and establishes territory after pairing. The residents prevent other coots from approaching or entering their territories, and also indulge in aggressive behavior against other species of birds during most time of the breeding period.

Ducks took up the main part in interspecific conflicts' list, especially for the Common Pochard (*Aythya ferina*), which was attacked violently by the coots frequently (Table 1). The Great Crested Grebe was left quite unmolested compared with Little Grebe (*Tachybaptus ruficolli*) which would be driven out when approaching the coots' territories. However, both of them were permitted to breed in the immediate vicinity of the coots nest. The nearest distance was only about three meters away from the coot's nest (Table 1). Black-winged Stilt (*Himantopus himantopus*) was also found to nest near the coot. Meanwhile, the coots constructed the nests in the nest areas of Black-necked Grebe (*Podiceps nigricollis*) and Black-headed Gull (*Larus ridibundus*).

Interspecific aggression started after pairing, and got severe until incubation. During incubation, other species were more tolerant within the territorial areas than in the immediate vicinity of the nest. As the young got older and more independent, the parents became less aggressive toward other species. Grebes together with their young birds moved freely in the territory of coots without any other attacks.

On May 10, a pair of the Common Pochards swam to the nests of the coot. After the female laid in the nests, they were driven away by the coot in 14 min. However, one day later, a pair of pochards appeared in the coots' territory again. The female had been lying in the nest for 18 min until the coots got back and drove them away. One hour later, around the same area a pair of pochards followed by another male approached the coot's nests slowly and vigilantly. Once they arrived, the female laid in the nest. After a while, the other male flew away, but 4 min later the coots came back and drove them away. We can't confirm whether they were the same pair.



Table 1. Interspecific conflicts of the breeding population of the coots

Curacias conflict with the costs	Family	Genus	Observed time	Nest distance to the coots' (m)	
Species conflict with the coots			(Day)	Mean (N)	Rang
Common Moorhen (Gallinula chloropus)	Rallidae	Gallinula	4	_	_
Common Pochard (Aythya ferina)	Anatidae	Aythya	7	_	_
Mallard (Anas platyrhynchos)	Anatidae	Anas	1	176.000±58.506 (n=3)	59-236
Gadwall (Anas strepera)	Anatidae	Anas	2	_	_
Common (ShoVeller Anas clypeata)	Anatidae	Anas	1	_	_
Little grebe (Tachybaptus ruficolli)	Podicedidae	Tachybaptus	3	25.125±4.138 (n=8)	5-41
Great Crested grebe (Podiceps cristatus)	Podicedidae	Podiceps	1	14.809±2.373 (n=21)	3-46
Black-winged Stilt (Himantopus himantopus)	Recurvirostridae	Himantopus	1	73.200±3.878 (n=5)	59-79
Black-headed gull (Larus ridibundus)	Laridae	Larus ridibundus	_	53.667±2.848 (n=30)	6-57

Variety of territory behaviors in different periods of reproduction The territory activities of nine pairs of the coots in different breeding periods were observed and recorded completely, including "fighting, warning, expelling (to drive away neighbors or floaters), invasion (to invade the neighbors' territories, when they were absent from the invasion sites) and expelling other species. The results indicated that the trend of territorial activities in three periods of breeding decreases ($R^2 = 0.648$, p = 0.009), and the differences of territorial activities in three periods of breeding are very significant ($\chi^2 = 9.953$, df = 2, p = 0.008). Territory behaviors were most frequent behaviors in the nest building period, and would decrease until laying eggs (Fig. 1). During the whole reproduction, warning was the most frequently adopted behavior pattern compared with others (Fig. 2). With the progress of reproduction, the coots seldom fought with each other and the invasion took place only in the nest building period because the territorial boundaries were not stable.

When the coots were in hatching, the territory activities decreased obviously. Sometimes, the pairs maintained good relationship with their neighbors without any conflicts within the whole day. The voluntary invasion into others' domains decreased in the laying stage and eventually disappeared in incubation stage (Fig. 2). Expelling other species lasted throughout all the three breeding periods. When the coots were in brooding, the territory defense activities were mostly expelling and warning. Fighting decreased sharply compared with expelling and warning. The immature coots were treated as territory invaders when they were independent.

Territory size

In the study, the territory sizes of 11 pairs of coots were obtained (Table 2). The average area estimated by quadrat was shown in Table 3. The difference of territory size between each pair was significant (t = 20.603, df = 10, p < 0.001). The territory size of F. atra ranged from 1 333 m² to 6 324 m². The distance from the coot's nest to their nearest neighbors was measured. There were significant correlation (r = 0.594, p = 0.012, n = 17) between territory size and nests distance (Fig. 3). Due to the large number of nests with suitable vegetation cover, the territory size of coots was small accordingly.

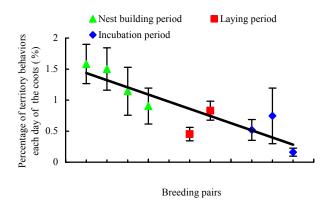


Fig. 1 Mean proportion of the territory behaviors of the coots each day in different breeding period.

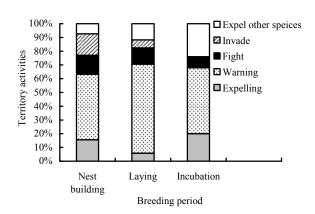


Fig. 2 Composition of territory activities in different periods of breeding.

In autumn, as most of the coots finished brooding, the young birds became more independent, the areas protected were considerably smaller than that in earlier for the pairs, whose territory was adjacent to the open water. Territorial boundaries were draw back to the edge of vegetation. The water surface in the territories seemed not to be protected by the pairs.



Table 2. Territory size of the coots: 11 pairs of the coots observed in breeding season.

Location	Code of breeding pair	Observation time (h)	Breeding period	Territory area (m²)	Nest distance (m)
Anbanghe	A	94	Nest building	5066	37
Anbanghe	В	94	Nest building	3543	37
Anbanghe	C	93	Nest building	4860	25
Anbanghe	D	92	Nest building	4119	54
Anbanghe	E	90	Laying eggs	>5000	41
Longfeng	F	93	Laying eggs	3754	36
Longfeng	G	60	Incubation	3458	36
Longfeng	Н	58	Incubation	3365	43
Longfeng	I	58	Incubation	5076	48
Longfeng	J*	40	Incubation	4240	29
Longfeng	K*	40	incubation	4853	29

Table 3. Territory size of the coots: average territory size of each pairs of the coots in six sample areas.

Code	Acreage (m ²)	No. of nest pairs	Territory area (m ²)	Nests distance (m)	Coverage (%)
YF1	13000	7	1857	20.80±3.9799 (9-31)	90
YF2	14000	6	2333	23.00±7.08284 (14-44)	60
YF3	20000	9	2222	24.43±4.62837 (13–42)	40
YF4	14000	12	1333	21.25±3.65841 (7–37)	70
DQ	94000	17	5529	47.73±4.91952 (23–79)	20
YJ	71000	17	4176	25.36±5.72915 (5–56)	20

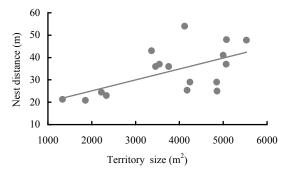


Fig. 3 Correlation of territory size and the nest distances.

No territoriality in winter

In Poyang Lake of Jiangxi Province, the coots gathered in the open water. They got along well with each other and other specie without any conflicts in the shallow water. The coots were always living harmoniously with swans, ducks, grebes and the snipes, which were never been invaded in winter.



Variation of territory behaviors in one year

F. atras arrived at Anbanghe NNR and Longfeng wetland in late March or early April. They flocked in the open water without territoriality until late April or early May. The coots paired, dispersed into vegetation areas, showed aggressive behaviors against other individuals, and began to establish their own territories. Correspondently the coots secured and guarded their territory by calls and territory activities. During May, an upsurge in territorial activity became evident, and the conflicts became increasingly frequent and severe. In June, there were fewer territorial behaviors for most cooks, especially for those whose energy and attention were concentrated on the brooding. But there were still several pairs expanding territories or beginning to lay eggs. The population still kept high level of territory activities. The ponds in Anbanghe and Longfeng Wetland became more peaceful since July, when nearly all the cooks finished incubation and were bringing up young coots. Territory behavior disappeared gradually until the young were independent enough. In September, the sub-adults gathered in the open water to prepare for migration which began from late September until late November. For the wintering population, they arrived at the wintering ground (Poyang Lake) in October. There were no territory behaviors during the wintering period. F. atras began to migrate in March (Fig.4).

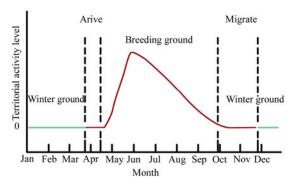


Fig. 4 Variation description of territorial activity level of the migrating *F. atra* in a whole year.

Discussions

Interspecies conflicts

Cramp (1947) summarized that the Coots were found to attack other species from time to time. Nylund (1945) stated that the coots, both male and female, regularly drove intruding ducks away from their own territory. The coots were more easily irritated by ducks. In the present study, ducks frequently emerged in the coots' territories compared with the other species, especially the Common Pochard, they occupied the coots' nests and platforms for the purpose of loafing. Both Bennett (1938) and Low (1941) noted that Blue-winged Teal and Ruddy Ducks occupied coot structures for their own use. Gullion (1953) found that the

reason why coots attacked ducks more frequently was that the American Coot's unused structures (usually brood nests) were taken over by Mallard hens to brood ducklings. In Anbanghe and Longfeng wetlands, because the nest sites of the Black-headed gull were located in deep cattails, the observation was more difficult. The conflicts between the Black-headed gull and coots were not recorded, which did not mean that they got along well with each other. *F. atra* was reported to eat the Black-headed Gull's eggs (Densley 1966).

Different territory size between pairs

Territory size is one of the major characteristics of territoriality (Finck 1990). Cramp (1947) worked out the areas for the secure territories of seven pairs of *F. atras* in England, and the average area was about 3 480 m², with a range from 2 024 m² to 4 452 m², which was similar to that obtained for *F. atra*. Territory size could be considered as the competition outcome between the owner and its neighbors for the resource units in the defended area (Petrie 1984). Territory size also has functions as the intruder's pressure, since the increasing food levels attracts more competitors (Hixon 1980; 1982; Schoener 1983).

The size of territories definitely varies with the density and distribution of suitable nesting coverage, and could be dependent upon three possible asymmetry factors; (1) difference in resource holding potential (RHP); (2) difference in resource value to the competitors; (3) difference in "ownership" status (Petrie 1984). Territory size can be considered as the competition outcome between the owner and its neighbors for the resource units in the defended area. The stronger one was always in a dominant position. They competed with others, and then occupied larger and more quantity territory as a result.

Territory density was affected by the vegetation coverage, but the coots avoided nesting in dense dry cattails. Pairs who occupied better habitat reproduced earlier. Pairs, whose territory was at the edge of ponds without enough coverage, always delayed laying egg until new vegetation grew up. Their territory was larger than those, whose territories were in the center, and confronted fewer competitions. Distribution and quality of resources affects the attractiveness of different parts of a territory on both residents and intruders, because the animals are willing to acquiring and defending valuable resource sites (Johnsson et al. 2000; Gray et al. 2002). In a pond of Anbanghe Nature Reserve, whose area was as large as 1.0×10^5 m² with little cover, only two nests located in two sparse reeds were found in 2008 and 2009 respectively. Some floaters sometimes emerged in the pond, since there was not enough cover to support more pairs.

Variety of territory behaviors in the year

Assessing fighting ability was thought to benefit territorial neighbors by allowing them to avoid the potential costs of escalated fights (Smith et al. 1973). Therefore, the relationships between established neighbors are often expected to become less aggressive over time, and neighbors will show lower aggression towards each other than towards unfamiliar individuals (Stamps

et al. 1997). In May, most coots began to build platforms and nests, and the territory was established but still not stable. And the coot always invaded into the neighbors' territories, leading to more frequently defense activities than the other time. Animals often faced trade-offs during reproduction between activities such as parental care and territory defenses (Ioana et al. 2007). The coots paid more energy on caring for eggs and incubation after May. The territory borders were confirmed by conflicts before, and the relationships between established neighbors were less aggressive, especially in the hatching period. In the most the time, only one coot in a pair could move freely, because the other one was engaging in incubation in the nest. Therefore, the number of the conflicts between neighbors was reduced accordingly. The reproduction time of females was not always the same, the earliest pairs finished incubation in early May; however, the latest ones just began to lay eggs in late June, and sub-adults still in parents' territories were expelled by the neighbors whose children were not independent. So, there were the territory behaviors in September. Differed from the resident population that still maintain territory in winter (Huxley 1934; Cramp 1947), the wintering population in Jiangxi Province of China did not show there are any conflicts in both intraspecies and interspecies.

The function of territory

The coots' food list contained many different kinds of water plants and animals, thus in the breeding season the coots had adequate food resources. The aggressiveness of F. atra toward other species, as well as the increased territorial behaviors to neighbors and floaters during the breeding season, seems not to be correlated with the defense of the food resources. In the brooding period, when more food was needed, the territory behaviors didn't increase correspondingly. Attacks against other species which were tolerant to nest in coots' territory could also hardly be correlated with the young defense or the food supply. The primary function of territory for the coots is probably reproduction, and the self-preservation is of less importance. It is thought that the food situation is incidental in coot territorialism. The factor of maintaining the pair bond is not a good cause to explain this question, maybe there are other functions of territory for coots.

In the field investigation, we found that a big portion of conspecific brood parasitism (CBP) between females in both two sites (unpublished data), and the platforms which were probably used to identify the territory boundary, were found to be mistakenly parasitized by other females. So we can infer that high aggressive territory behaviors might be caused by high epidemic of CBP, the patrol, and the protection of their nests and platforms from invasion by others. The territory activities were a defense of being parasitized, however, invading into the other's territory might be caused by the need of seeking opportunities to parasitized.

The Black-headed Duck (*Heteronetta atricapilla*) mainly parasitized just two species of coots, the Red-gartered Coot (*Fulica armillata*) and the Red-fronted Coot (*Fulica rufifrons*) (Phiilips 1925; Weller 1968; Lyon 2004), and the Ruddy Ducks (*Oxyura*



Jamaicensis) occasionally laid eggs in the American coot nests (Weller 1959; Fredrickson 1970). The Common Pochard was reported to parasitically lay their eggs in the nests of the Baer's Pochard (Aythya baeri) (Gao et al. 1992). By the observations, we found that in the most time, only female Common Pochard occupied in the coots' nest. And the reason why the female laid eggs in the coots' nest may be that they were seeking the opportunity to parasitize their eggs in the coots' nest. Even though interspecies brood parasitism (IBP) was not detected in F. atra, it is not impossible that the coot is the host of the Common Pochard

Acknowledgements

Thanks go to Anbanghe Nature Reserve and Longfeng Nature Reserve for permission to conduct this research. We are grateful to Daqing Wildlife Conservation Association for providing kindness help on room and board.

References

- Alisauskas RT. 1987. Morphometric correlates of age and breeding status in American Coots. Auk, 104: 640–646.
- Bennett LJ. 1938. The blue-winged teal, its ecology and management. Ames USA: Collegiate press, p144.
- Cavé AJ, Visser J, Perdeck AC. 1989. Size and quality of the coot *Fulica atra* territory in relation to age of its tenants and neighbours. *Ardea*, 77: 87–98
- Cramp S. 1947. Notes on territory in the coot. Brit Birds, 40: 194-198.
- Densley M. 1966. Coot eating Black-headed Gull's eggs. *Brit Birds*, **59**: 306
- Finck P. 1990. Seasonal variation of territory size with the Little Owl (Athene noctua). Oecologia, 83: 68-75.
- Fredrickson LH. 1970. Breeding biology of American Coots in Iowa. The Wilson Bulletin, 82(4): 445–457.
- Gao Jihong, Ma Jianzhang. 1992. The behavior of incompletes brood parasitism of two pochard species. *Zool Res*, **4**: 327–329 (in Chinese.)
- Gray SJ, Jensen SP, Hurst JL, 2002. Effects of resource distribution on activity and territory defence in house mice, *Mus domesticus*. *Animal Behaviour*, **63**(3): 531–539.
- Gullion GW. 1952. The display and calls of the American Coot. *The Wilson Bulletin*, 64: 83–97.
- Gullion GW. 1953. Territorial behavior of the American coot. The Con-

- dor, 55: 169-186.
- Hixon MA. 1980. Food production and competitor density as the determinants of feeding territory size. *The American Naturalist*, **115**(4): 510–530.
- Hixon MA. 1982. Energy maximizers and time minimizers: theory and reality. *The American Naturalist*, **119**: 596–599.
- Huxley JS. 1934. A natural experiment on the territorial instinct. *Brit Birds*, 27: 270–277.
- Hyman J, Hughes M. 2006. Territory owners discriminate between aggressive and nonaggressive neighbours. *Animal Behaviour*, 72: 209–215.
- Ioana C, Morton SE, Stutchbury BJM. 2007. Incubation delays territory defence by male blue-headed vireos, Vireo solitarius. *Animal Behav*iour, 73: 143–148.
- Johnsson JI, Carlsson M, Sundström LF. 2000. Habitat preference increases territorial defence in brown trout (Salmo trutta). Behavioral Ecology and Sociobiology, 48(5): 373–377.
- Low JB. 1941. Nesting of the ruddy duck in Iowa. Auk, 58: 506-517.
- Lyon BE, Eadie MJ. 2004. An obligate brood parasite trapped in the intraspecific arms race of its hosts. *Nature*, **432**: 390–393.
- Petrie M. 1984. Territory size in the moorhen (*Gallinula chloropus*): An outcome of RHP asymmetry between neighbours. *Animal Behaviour*, **32**(3): 861–870.
- Philips JC. 1925. A natural history of ducks. Vol.3. Houghton-Mifflin Co.,
- Ryan MR, Dinsmore JJ. 1980. The behavioral ecology of breeding American Coots in relation to age. *The Condor*, 82: 320–327.
- Schoener TW. 1983. Simple models of optimal feeding-territory size: a reconciliation. *The American Naturalist*, **121**: 608–629.
- Smith MJ, Price GR. 1973. The logic of animal conflict. *Nature*, **246**: 15–18.
- Stamps JA, Krishnan VV. 1997. Functions of fights in territory establishment. The American Naturalist, 150: 393–405.
- Stephan B. 1976. Die evolutive Bedeutung der Territorialität bei Vögeln. *Falke*, **23** (9): 297–305.
- Tinbergen N. 1957. The function of territory. Bird Study, 4: 14-27.
- Visser J. 1988. Seasonal changes in shield size in the Coot. *Ardea*, **76**: 56–63
- Weller MW. 1959. Parasitic egg laying in the Redhead (*Aythya Americana*) and other North American Anatidae. *Ecological Monographs*, **19**: 33–365.
- Weller MW. 1968. The breeding biology of the parasitic Black-headed Duck. Living Bird, 7: 169–207.

